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Predicting demographically sustainable rates of adaptation

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Published in:

Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences

DOI:

[10.1098/rstb.2012.0289](https://doi.org/10.1098/rstb.2012.0289)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version

Publisher's PDF, also known as Version of record

Publication date:

2013

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Gienapp, P., Lof, M., Reed, T. E., McNamara, J., Verhulst, S., & Visser, M. E. (2013). Predicting demographically sustainable rates of adaptation: Can great tit breeding time keep pace with climate change? *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 368(1610), [20120289]. <https://doi.org/10.1098/rstb.2012.0289>

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S2 Dynamic state model – general framework

Dynamic programming was used to estimate the optimal timing of reproduction [1]. In the model, the optimal decision of when to start egg-laying depends on the state of the bird, the environment and the time of year. A key property of the environment of the great tit is that there is both day-to-day variation and year-to-year variation in temperature and food abundance. Furthermore, at the time a female has to decide when to start egg-laying no caterpillars are present yet. At the start of egg-laying, the date of the peak in food abundance is uncertain. A female can only use information from the current day and the past when deciding when to start laying.

State variables

The bird is characterized by two state variables: brood size and the age of its brood. Based on these states a female can be in four reproductive phases: non-breeding, egg laying, incubating or caring for dependent young. Both avian laying date and the time of the seasonal peak in food abundance are affected by temperatures. Females in our model use temperature cues to decide when to start laying. The fluctuating environment is characterized by two state variables: temperature, and temperature sum. Temperature influences the energetic costs of egg production and incubation. Temperature sum is used to calculate caterpillar biomass.

Decisions

In our model, decisions are made daily throughout the simulated period. Dependent on the reproductive phase it is in, the bird has the following options. If an individual is not breeding it can continue not breeding, or start egg laying. If the bird is in the egg laying phase it can lay one more egg, start incubating or abandon the nest. If the brood size has reached its maximum, an individual can only start incubating or abandon the nest. If the bird is incubating, it can continue incubating, or abandon the nest. If the bird incubated for 12 days, the eggs hatch and the bird starts caring for its young. When it is caring for its young, it can continue care or abandon the nest. When the bird is not able to find enough food for its own energy expenditure and the energy need of its complete brood, it can decide to let one or more nestlings die and continue to care for the remaining nestlings. When the chicks reach the age that they fledge, the chicks become independent and the parent becomes non-breeding again. The optimal decision each day depends on the state of the bird, the environment (current temperature and temperature sum) and the time of year.

Temperature model

Weather states are persistent over short time scales above the seasonal temperature variation: a relatively warm day is more likely to be followed by another warm day than by a cold day, and vice versa. In other words, day-to-day changes in temperature are dependent on the current temperature. If the current temperature is close to the expected value for that day, it has an equal probability that the temperature the following day is higher or lower. However, if the deviation from the expectation is more extreme it will have a higher probability to return to the mean the following day. We used a ‘regression toward the mean’ approach to model daily temperature changes. In this model, $q(t)$ is the current temperature at day t , $q_{avg}(t)$ is the average temperature at day t over a 30-year temperature profile (see § *Scenarios explored* below). The temperature at the next day is calculated by

$$q(t + 1) = q_{avg}(t + 1) + \delta \left(q(t) - q_{avg}(t) \right) + \mu_q(w) + \sigma_q(w)r_q \quad (\text{eq. 1})$$

where $\mu_q(w)$ is the mean day-to-day variation (in general, $\mu_q(w)=0$), calculated per week w , $\sigma_q(w)$ is the standard deviation of the day-to-day variation in week w , and r_q is a normally distributed random number with mean=0 and variance=1. The parameters $\mu_q(w)$ and $\sigma_q(w)$, are estimated from the daily temperature for each 30-year period used (see § *Scenarios explored* below and S3). The variable δ controls the strength of the correlation of the current temperature and the temperature the following day. This strength is dependent on the deviation from the mean, and calculated by

$$\delta = 1 - \alpha \left(q(t) - q_{avg}(t) \right)^2 \quad (\text{eq. 2})$$

where $\alpha(q(t) - q_{avg}(t))^2$ calculates the strength of the autocorrelation. If the deviation from the mean is small the autocorrelation is high, if the deviation from the mean is larger the autocorrelation is smaller.

Food availability

The development of the caterpillars is temperature dependent. The seasonal caterpillar peak is earlier in warmer years [2]. Based on caterpillar biomass data from 1993-2009 [2], we developed a temperature degree-day model to predict caterpillar biomass. We first calculate the daily temperature sum, $s(t)$ by,

$$s(t) = \sum_{t_0=67}^t \max(0.0, T(t) - T_d) \quad (\text{eq. 3})$$

The best predictor for the timing of the caterpillar peak is the average temperature over the period from 8 March to 17May [2]. Therefore, we start at the 8 March ($t_0 = 67$) and add all temperatures higher than T_d °C. We used the temperature sum to predict the caterpillar biomass (see S3),

$$g(s) = \frac{A_F}{\sqrt{2\pi\sigma_F^2}} e^{-\frac{(s-\mu_F)^2}{2\sigma_F^2}} \quad (\text{eq. 4})$$

where s is the temperature sum, A_F adjusts the height of the caterpillar biomass, σ_F adjust the width of the caterpillar peak, and μ_F is the temperature sum at which the caterpillar biomass is highest.

Energy balance

To prevent death by starvation, a small bird must balance its energy expenditure and its energy intake every day [3]. In our model daily energy expenditure is dependent on the reproductive state of the bird, and on the state of the environment – food availability and temperature. An individual gains energy by foraging. To enable a direct link between food availability and daily energy expenditure (DEE) of the adult bird, we converted the estimated caterpillar biomass into available energy in the environment on one day (see S3). The energy in the environment that can be gathered in one day depending on the caterpillar biomass in the environment is calculated by,

$$E_{cat}(s) = \frac{A_E}{1 + e^{-\beta_E(g(s)-\gamma_E)}} \quad (\text{eq. 5})$$

where $g(s)$ is the caterpillar biomass, A_E sets the upper limit of the sigmoid function, β_E adjusts the steepness of the increase and γ_E is the biomass density at which the function switches from increasing with an accelerating speed to increasing with a decelerating speed. The daily intake of energy is $E(s)u$, with $E(s)$ the available energy in the environment in one day for temperature sum s (see S3), and u the proportion of the day spent collecting food.

Non-breeding phase

For a non-breeding individual its daily energy expenditure (DEE) is given by

$$DEE_{nb} = RMR(T) + uh \quad (\text{eq. 6})$$

where $RMR(T)$ is the temperature dependent resting metabolic rate [4,5], and h is the additional rate of energy expenditure due to the effort of foraging (e.g. during flight and active search).

$$RMR(T) = m_1 + m_2 * \max(0, (T_t - T)) \quad (\text{eq. 7})$$

The parameter T_t is the lower threshold temperature of the thermal neutral zone. Below this value the resting metabolic rate increases. Above this value $RMR(T) = m_1$.

Since energy intake and expenditure must balance, we have $E(s)u = RMR(T) + uh$, thus

$$u = RMR(T)/(E(s) - h) \quad (\text{eq. 8})$$

Egg laying phase

For producing eggs an extra amount of energy Δ_{egg} is needed. The daily expenditure of an individual in the egg laying phase is therefore given by

$$DEE_{egg} = RMR(T) + \Delta_{egg} + uh \quad (\text{eq. 9})$$

The fraction of time spend to maintain energy balance is calculated by,

$$u = (RMR(T) + \Delta_{egg})/(E(s) - h) \quad (\text{eq. 10})$$

Incubating phase

Incubating a nest expends energy Δ_{incday} during the working day and $\Delta_{incnight}$ during the nights. Furthermore, incubation cost is temperature dependent. To keep the eggs warm, birds expend more energy for lower temperatures. The daily energy expenditure of an individual in the incubation phase is given by

$$DEE_{inc} = RMR(T) + \Delta_{incnight}(T) + (1 - u)\Delta_{incday}(T) + uh \quad (\text{eq. 11})$$

with,

$$\Delta_{incnight}(T) = (i_1 - i_2T)(1 - f)$$

$$\Delta_{incday}(T) = (i_3 - i_4T)f$$

where f is the working day in hours. When a female is incubating she spends a large fraction of the working day incubating at the nest. In our model we assume that a female has 40% of the working day available for foraging. The energy balance of an incubating female is given by,

$$E(s)u = RMR(T) + \Delta_{incnight}(T) + (1 - u)\Delta_{incday}(T) + uh \quad (\text{eq. 12})$$

The fraction of the working day that an incubating bird should spend foraging to balance its energy expenditure is then calculated by,

$$u = \frac{RMR(T) + \Delta_{incnight}(T) + \Delta_{incday}(T)}{E(s) + \Delta_{incday}(T) - h} \quad (\text{eq. 13})$$

Chick rearing phase

When a female is caring for dependent young she not only has to balance her own energy expenditure, but also has to gather enough food to feed her young.

$$DEE_{care} = RMR(T) + u_{tot}h \quad (\text{eq. 14})$$

where u_{tot} is the total fraction of the working day that is needed to gather enough energy for her own maintenance and the energy needs of her dependent chicks. The energy need of the complete brood is given by,

$$DEE_{brood} = n(f(a), c, T)c \quad (\text{eq. 15})$$

where $n(f(a), c, T)$ is a function that calculates the energy need per chick that depends on the age of the chicks, a , the brood size, c , and on temperature, T . Therefore, u_{tot} can be calculated by

$$u_{tot} = \frac{RMR(T) + n(f(a), c, T)c}{E(s) - h} \quad (\text{eq. 16})$$

The energy intake of nestlings, $f(a)$, is age dependent. The energy need of a recently hatched nestling starts of low, but increases rapidly up to an age of 10 days, after which the energy need remains the same [6,7]. This pattern can be described by,

$$f(a) = \frac{A_y}{1 + e^{-\beta_y(a - \gamma_y)}} \quad (\text{eq. 17})$$

This relationship for energy intake is based on nests with 8 young (Fig. 6 in [6]). Royama [6] found an inverse relationship between food consumption per young and brood size (Fig. 15 in [6]). Moreover, Royama [6] found that food consumption is higher in early broods than in late broods. We assume that this is caused by temperature differences. Furthermore, at low temperatures the energy needs of small broods increases due to higher heat-loss [8]. Large broods have a better heat-regulation thus we expect no higher energy need at lower temperatures. We assume that at high temperatures all brood sizes have approximately the same energy needs per chick. Taking into account the relationships found by [6] and the above assumptions, the energy need, $n(a, c, T)$, per nestling can then be given by,

$$n(a, c, T) = (-y_1T + y_2)f(a)c^{(y_3T - y_4)} \quad (\text{eq. 18})$$

where y_1, y_2, y_3, y_4 are parameters that control how the energy need of one nestling depends on temperature and clutch size.

Sources of mortality

In our model we consider two sources of mortality: predation and starvation. Adult predation is linked to the fraction of the working day that a bird spends foraging and occurs with probability $d(u+u)^2$. If a bird cannot balance its energy expenditure and energy intake for one day it dies of starvation. A bird that is egg laying, incubating or chick rearing can always abandon the brood and thereby reduce the probability that it will starve. Furthermore, during chick rearing it can reduce the brood size (by letting one or more chicks starve) when there is not enough energy in the environment for its own maintenance and its' the energy need of its brood.

Fitness

To calculate the optimal decisions we need to specify the terminal reward function, which here depends on the survival of the female, the number of young that fledge and the date that the young fledge. Empirical

studies of Dutch great tits show that the probability that an fledged young recruits into the breeding population the next year decreases during the season [9,10,11]. We assume that the recruitment probability is the highest if the young fledge at the food peak. The timing of the peak in caterpillar biomass $g(s)$ is not a fixed date but depends on the temperature sum. To synchronize the highest recruitment probability with the peak date of the caterpillar biomass, the value for one young $v(s)$ is calculated by

$$v(s) = \frac{A_v}{\sqrt{2\pi\sigma_v^2}} e^{-\frac{(s-\mu_v)^2}{2\sigma_v^2}} \quad (\text{eq. 19})$$

where s is the temperature sum, A_v adjusts the height of the maximum recruitment probability, σ_v adjust the width of the normal distribution, and μ_v is the average temperature sum at the peak date in caterpillar biomass (thus $\mu_v = \mu_F$) where the recruitment probability is highest.

Scenarios explored

To investigate the change in the optimal laying dates between 1951 and 2100 under three climate scenarios, with a ‘mild’ a ‘medium’ and an ‘extreme’ temperature increase, we divide the total period of interest in 13 periods of 30 years (with a shifting time window of 10 years, i.e. 1951-1980, 1961-1990, 1971-2000 etc.). The Royal Netherlands Meteorological Institute (KNMI) provided us with 17 simulated time series of daily average temperatures from 1951-2100 of the IPCC SRES A1B scenario (the ‘mild’ scenario). We used these 17 time series to compute the scenarios with ‘medium’ and ‘extreme’ temperature increase (see paragraph Climate change scenarios in main text). For each of the 3 scenarios, each of the 17 replicates and each of the 13 periods we parameterized the temperature model for the optimization model and the Monte Carlo forward simulations with the average daily temperature and the day-to-day variation of that period. To calculate the change in optimal laying date we ran 1,000 Monte Carlo forward simulations per period×replicate×scenario.

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